The Ecology of Jamaican Coral Reefs I. Species Composition and Zonation

Thomas F. Goreau

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sis during the cold season, whenever the environmental conditions are favorable.

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THE ECOLOGY OF JAMAICAN CORAL REEFS
I. SPECIES COMPOSITION AND ZONATION[1]

THOMAS F. GOREAU
Physiology Department, University College of the West Indies and The New York Zoological Society

INTRODUCTION

This paper, the first of a series, is intended to serve as a descriptive introduction of the corals of Jamaica, and to give the results of a preliminary survey of zonation and growth forms of scleractinian populations on Jamaican reefs.

The investigation of Jamaican corals began with Sir Hans Sloane (1707) and Dr. Patrick Browne (1756) who figured a number of "zoophyta" in their respective natural histories of the island. However, the systematic study of Jamaican corals did not begin until Duerden (1902, 1904) published his classic monographs on the structure, development and biology of West Indian madreporaria, most of which he collected near Kingston and Port Royal. Unfortunately, Duerden gave little information on localities and none on ecological relationships, and made no attempt to describe the reef habitat as a whole. The madreporarian collection at the Institute of Jamaica (Fontaine 1954) includes some of Duerden's specimens, but it is still incomplete at the time of writing.

During the past three years, the author has had the opportunity to carry out a series of field and laboratory investigations on Jamaican reef building corals. A complete collection has been assembled, which will eventually be deposited at the United States National Museum.

[1] A part of the material in this paper was taken from a doctoral dissertation submitted by the author to Yale University.

West Indian reefs in general, and Jamaican reefs in particular, are on the whole very much smaller than their Indo-Pacific counterparts. Nevertheless, Colman's assertion (cf. Steers 1940 p. 306) to the effect that "Jamaican reefs are far from typical coral formations" and the further implication that most of them are not holding their own is based, as will be seen below, on incomplete evidence derived from observations carried out on a small number of reefs which happened to be located in that part of Jamaica visited by the Cambridge Expedition of 1939. Whereas the number of scleractinian species in West Indian reefs is at best less than one third that known to occur, for example, on the Great Barrier Reef or in the Marshall Islands (Wells 1954), the density of coral growth is in many localities comparable. Also, the calcareous algae which form between forty and ninety per cent of the reefs in Bikini Atoll (cf. Johnson 1954), play a very much less conspicuous role in the building up and consolidation of West Indian reefs. For a comparison of zonation and species composition of reefs in several Pacific atolls the reader is referred to the papers of Wells (1951, 1954) and Emery *et al.* (1954).

METHOD

The methods used in the ecological study reported in this paper were extremely simple. The reefs described were readily accessible by small boat during calm weather. Initial transects were run by swimming across the reef with fins, mask, breathing tube, and a geological hammer with which to collect specimens. In this way, the reef could be observed to depths of about fifteen meters. Detailed transects were run with the aid of a sounding line marked off in meters, and the approximate number of corals of different species in the range of vision at various stations was noted. Underwater photographs were taken in representative areas and sketches and field measurements were recorded on an underwater drawing board made of roughened white plexiglass. The great majority of the field observations were carried out by mask diving, but some work in deeper parts of certain localities had to be done with the aid of a self contained diving unit of the oxygen recirculator type. In Barbados, most of the reef surveys in deeper waters were made with an Aqualung.

Grateful acknowledgments are due to the following: Professor D. M. Steven of the Zoology Department of the University College of the West Indies, for making available a boat and other facilities of the University's Marine Station in Port Royal; Mr. Lachlan Macneil, Ocho Rios, for his personal interest and assistance in surveying the Ocho Rios reefs; Dr. V. A. Zans and Professor Normal Newell for stimulating discussions of certain points of geological interest; Captain E. G. Irving, O.B.E., R.N. for kindly making it possible to carry out aerial photosurveys of some Jamaican north coast reefs from the helicopter of H. M. Admiralty Survey Ship *Vidal;* Dr. Arthur Fontaine of the Institute of Jamaica who assisted with the initial identification of some of the coral species; Dr. John Lewis, Director of the Bellairs McGill Research Institute in Barbados for his hospitality and help during a short trip to the eastern Caribbean that was supported by an institutional grant from funds provided by the Carnegie Foundation. Much of the work reported in this paper was supported by a grant from the New York Zoological Society. The geological map shown in Figure 1 is reproduced with the kind permission of Dr. V. A. Zans, Director of the Geological Survey of Jamaica.

General Description of Jamaica

Jamaica is a large tropical island about 125 miles long and 50 miles wide, 18° 30′ degrees north of the equator. It is located in the center of the Carribean area just south of Cuba and west of Hispaniola.

Geologically, the island is a low dome built up on a core of upper Cretaceous rocks which are unconformably overlain by a sedimentary mantle ranging in age from Eocene to Recent (V. A. Zans, private communication). More than two thirds of the surface is covered by limestones of different kinds. The coastal formations on the north shore are mainly hermatypic limestones of Miocene to Pleistocene age, whereas the south shore is built up of older limestones and extensive Recent alluvial deposits that fan out from the central highlands (see Figure 1).

Along the greater part of the coastline, the offshore shelf is relatively narrow so that the 20-fathom contour lies mostly less than 500 meters from land except in the region between Kingston and Black River where there is a large offshore shelf 15 miles wide by about 80 miles long.

Jamaica lies in the belt of the northeasterly tradewinds, but the island is large and high enough so that a semi-continental climate exists in the interior. Local factors combine to alter considerably the pattern of the prevailing surface winds in different parts of the island. According to Pilsbury (1951) 90% of the surface winds above 15 miles per hour at Palisadoes Airport on the south coast near Kingston blow from a southeasterly direction. On the other hand, on the northwest coast at Montego Bay Airport, surface winds above 15 miles per hour blow from a northeasterly direction about 75% of the time.

The surface temperature of coastal waters varies between 24°C in January and 27.5°C in July. Higher temperatures are often encountered in harbours and lagoons where circulation is restricted. The tides are irregular, tending to "double up" so that they occur only once a day. They vary in height between 20 and 36 centimeters. There is a well defined westward current on both coasts which becomes more pronounced during the trade wind season between April and December.

The geographical distribution of reef tracts on the coast of Jamaica and their relation to the underlying geology is shown in the map in Figure 1. On the north coast, fringing reefs extend, with some gaps, from Morant Point in the east to Negril in the west. On the south coast however, large reefs are restricted to the eastern part of the coastal shelf near Port Royal and Old Harbour. Elsewhere on this coast reefs tend to be small, patchy and often dead.

The Jamaican Scleractinian Fauna

Of the 41 scleractinian species so far collected in Jamaica, 40 have been found by the writer and 14 are new records. Only one, *Solenastrea bournoni,* which was listed by Duerden (1902) as occurring in Kingston Harbour, has not yet been

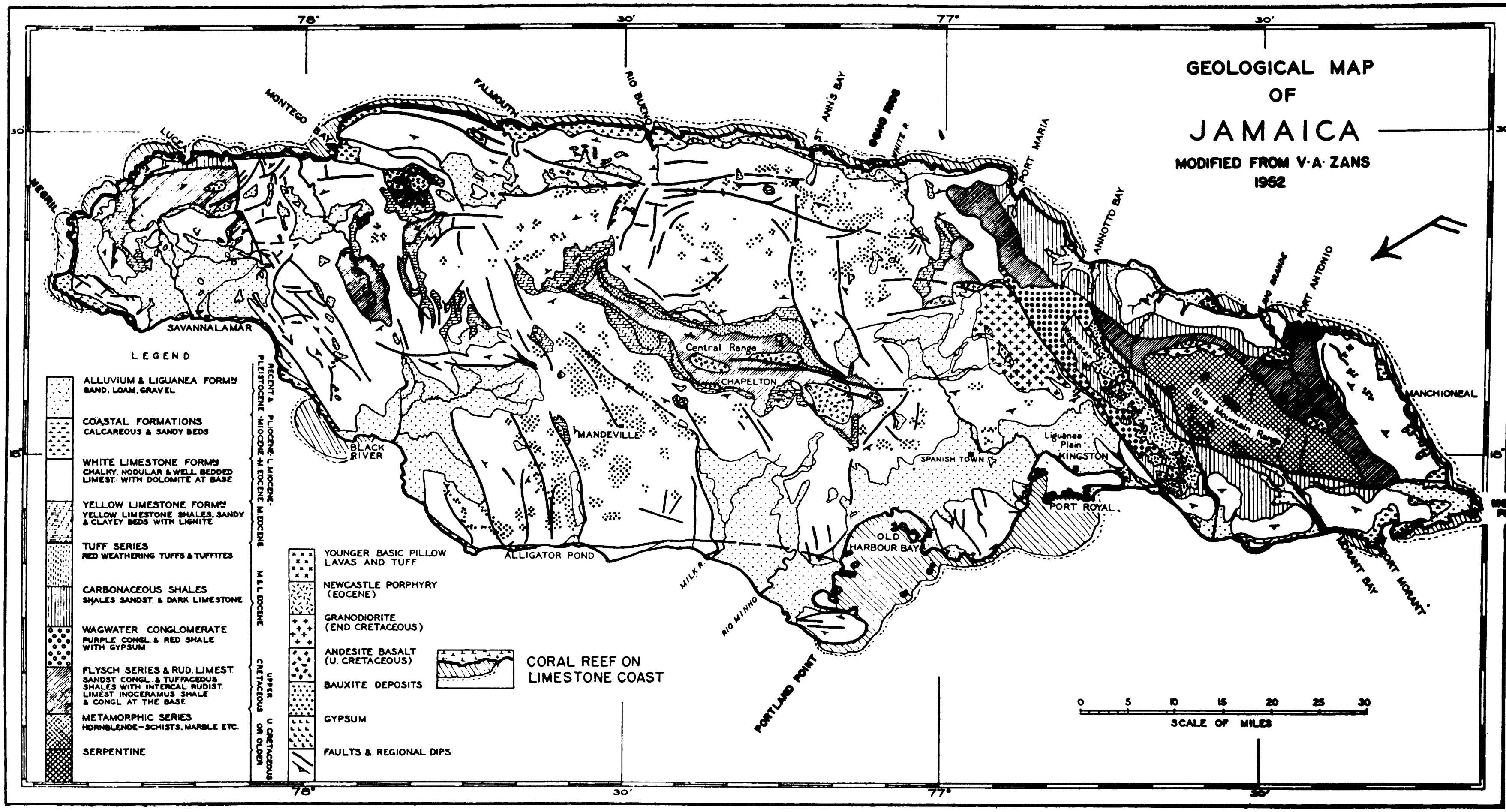

FIG. 1. Geological map of Jamaica showing the dome structure of the island with successively younger sedimentary formations at the periphery. The cross hatched parts of the seacoast represent areas in which large coral reefs are found. The map is by courtesy of Dr. V. A. Zans and the Jamaica Government Geological Survey.

TABLE I. List of Jamaican Shallow Water Scleractinia*†

Class ANTHOZOA Ehrenberg
Subclass HEXACORALLIA Haeckel
Order SCLERACTINIA Bourne
Suborder ASTROCOENIINA Vaughan and Wells
Family ASTROCOENIIDAE Koby
Stephanocoenia michelinii (Milne Edwards and Haime)[D,G]
Family ACROPORIDAE Verrill
Acropora palmata (Lamarck)[D,G]
Acropora cervicornis (Lamarck)[D,G]
Acropora prolifera (Lamarck)[D,G]
Family POCILLOPORIDAE Gray
Madracis decactis (Lyman)[G]
Madracis asperula (Milne Edwards and Haime)[G]
Suborder FUNGIINA Duncan
Superfamily AGARICIICAE Gray
Family AGARICIIDAE Gray
Agaricia agaricites (Linnaeus)[D,G]
Agaricia fragilis (Dana)[D,G]
Agaricia nobilis (Verrill)[G]
Family SIDERASTREIDAE Vaughan and Wells
Siderastrea siderea (Ellis and Solander)[D,G]
Siderastrea radians (Pallas)[D,G]
Superfamily PORITICAE Gray
Family PORITIDAE Gray
Porites porites (Pallas)[D,G]
Porites astreoides (Lamarck)[D,G]
Porites furcata (Lamarck)[D,G]
Porites divaricata (Lesueur)[D,G]
Suborder FAVIINA Vaughan and Wells
Superfamily FAVIICAE Gregory
Family FAVIIDAE Gregory
Subfamily FAVIINAE Gregory
Favia fragum (Esper)[D,G]
Diploria strigosa (Dana)[D,G]
Diploria clivosa (Ellis and Solander)[G]
Diploria labyrinthiformis (Linnaeus)[D,G]
Colpophyllia natans (Muller)[D,G]
Colpophyllia amaranthus (Muller)[G]
Manicina areolata (Linnaeus)[D,G]
Subfamily MONTASTREINAE Vaughan and Wells
Cladocora arbuscula (Lesueur)[D,G]
Montastrea annularis (Ellis and Solander)[D,G]
Montastrea cavernosa (Linnaeus)[D,G]
Solenastrea hyades (Dana)[D]
Family RHIZANGIIDAE d'Orbigny
Astrangia solitaria (Lesueur)[D,G]
Phyllangia americana (Milne Edwards and Haime)[D,G]
Family OCULINIDAE Gray
Subfamily OCULININAE
Oculina diffusa (Lamarck)[D,G]
Oculina valenciennesi (Milne Edwards and Haime)[D,G]
Family MEANDRINIDAE Gray
Subfamily MEANDRININAE Gray
Meandrina meandrites (Linnaeus)[D,G]
Meandrina braziliensis (Milne Edwards and Haime)[G]
Subfamily DICHOCOENINAE Vaughan and Wells
Dichocoenia stokesii (Milne Edwards and Haime)[D,G]
Dendrogyra cylindrus (Ehrenberg)[G]
Family MUSSIDAE Ortmann
Mussa angulosa (Pallas)[G]
Isophyllia multiflora (Verrill)[G]
Isophyllia sinuosa (Milne Edwards and Haime)[D,G]
Isophyllastrea rigida (Dana)[G]
Mycetophyllia lamarckana (Milne Edwards and Haime)[G]
Suborder CARYOPHYLLIINA Vaughan and Wells
Superfamily CARYOPHYLLIICAE Gray
Family CARYOPHYLLIIDAE Gray
Subfamily EUSMILIINAE Milne Edwards and Haime
Eusmilia fastigiata (Pallas)[G]
Suborder DENDROPHYLLIINA Vaughan and Wells
Family DENDROPHYLLIIDAE Gray
Tubastrea tenuilamellosa (Milne Edwards and Haime)[G]

* Classification is according to Vaughan and Wells (1943) and Wells (1956).
† The symbols D and G in superscript following the species names indicate whether species was recorded by Duerden (1902), by Goreau, or by both.

recorded by the author. Of all the shallow water species listed in Table I, only 5, belonging to the families *Rhizangiidae, Oculinidae* and *Dendrophylliidae,* can be classified as ahermatypes despite the fact that they often grow in localities where hermatypes also occur.

The finding of *Meandrina braziliensis* in Jamaica is of some interest. Smith (1948) states that this coral is found in Floridian and West Indian reefs, but localities or references are not given. There is increasing evidence that this species is found in the deeper zones of the fore reef, or seaward slope. In Barbados it is common at depths below 5 meters. Last year some colonies were recovered from a submarine cable at a depth of about 40 meters just east of Turks Island. Small colonies were recently dredged by H. M. Admiralty Survey Ship *Vidal* from sandy bottom at 20 meters, 12 miles south of Milk River, Jamaica. *M. braziliensis* has not been seen growing in Jamaican reefs at the time of writing, but it is interesting to note that specimens of this coral have been found by Dr. V. A. Zans on boulder ramparts of the Pedro Cays 60 miles south west of Kingston.

Some observations on the distribution of *Tubastrea tenuilamellosa* are also of interest. In con trast to all other corals in this area which are predominantly green, yellow or brown due to their zooxanthellae, the coenosarc of *Tubastrae* is colored a bright red and zooxanthellae are absent. The clump-like colonies, which do not exceed 15 centimeters across, are sometimes found in restricted localities on very exposed coasts where they grow at shallow depths on wave swept rocks, usually together with some reef building corals. In both appearance and ecological requirements, *Tubastrea* bears an extraordinary resemblance to the Mediterranean dendrophylliid *Astroides calycularis.* No precise information is as yet available on the extent of distribution of this coral in West Indian waters as it has been previously reported only from Curacao (J. W. Wells, J. S. Zanevelt, private communication).

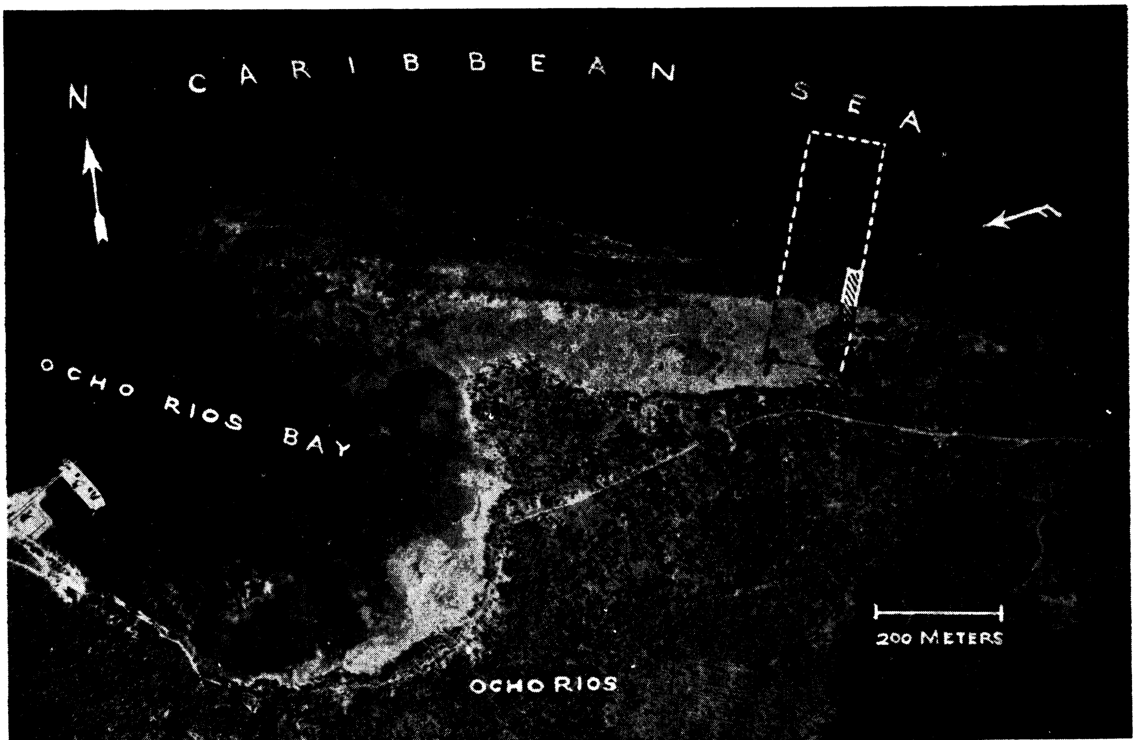

FIG. 2. Airphoto of the fringing barrier reef located north-east of Ocho Rios, Jamaica, and described in the text. The large cleft or canyon running diagonally through the center of the reef is an unique feature of unknown origin that is not seen in other Jamaican reefs. It appears to be unrelated to rivers or other physiographic features. The rectangle on the right hand side of the figure represents the area covered by Figure 3, and the smaller cross hatched rectangle is the region shown in Figure 5. Airphoto courtesy of the Jamaica Government Survey.

ZONAL ANALYSIS OF A LARGE REEF NEAR OCHO RIOS, JAMAICA

All larger Jamaican reefs can be divided into regions and zones on the basis of local differences in topography and species associations of corals and other bottom organisms. The reef to be described in this section is typical of the large fringing barrier reef communities found along the north coast of Jamaica; it is shown in the aerial photograph in Figure 2. This structure runs in an east-west direction at distances between 10 and 600 meters from shore and extends partly across the mouth of Ocho Rios Bay. The reef intercepts the trade wind seas tangentially so that wave action is moderate for the greater part of the year except during January, February and March when heavy seas may pound the coast during northerly gales. The transparency of the water in this area is variable, and depends largely on the degree of wind-generated turbulence which can reduce the visibility to a few meters on the fore reef and to zero in the channel or lagoon. Sediment carried into the sea by rivers also reduces the surface transparency of the water. The surface salinity may be noticeably decreased by fresh water welling into the sea from the base of the limestone cliffs which form much of the shore line of this coast. On calm days, lenses of brackish water can frequently be found on the surface several hundred meters offshore. This does not appear to have any untoward effect on coral growth except very close inshore where the cold upwelling ground water often reduces the salinity to such an extent that the water is nearly fresh to the taste.

The oxygen content of the water crossing the reef varies between 3.0 and 9.0 ml/L, depending on the light intensity, turbulence and sediment in the water. On the average sunny day, the water on the reef becomes supersaturated with oxygen as shown by the gas bubbles which collect on the coral and algae during calm weather. Our measurements show that in daytime the water crossing the reef gains between 0.6 and 2.5 ml O_2/L whereas at night about 1 ml O_2/L is removed by respiration.

The hydrography of these reefs is somewhat complicated by the fact that in the daytime the main driving force of the water circulation is provided by the easterly trade wind which sets up a longshore current that dies down at night with

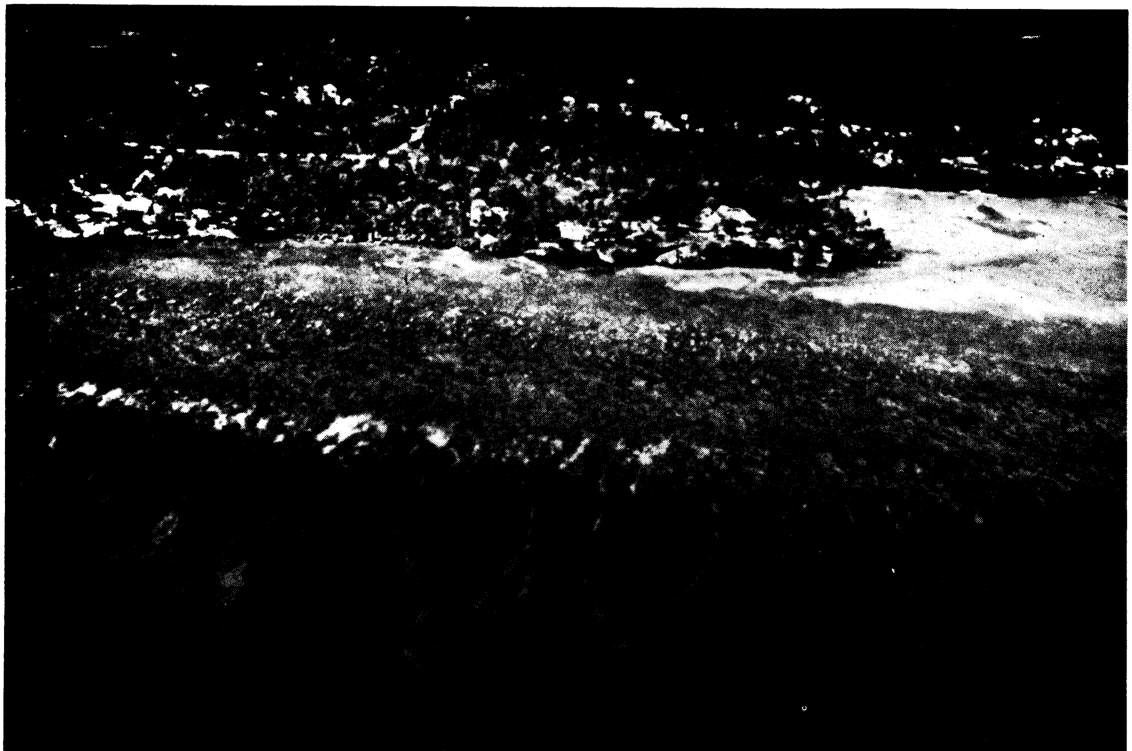

FIG. 3. Oblique airphoto of the fringing barrier reef at Ocho Rios, Jamaica, taken with polaroid filter and extreme wide-angle lens from a helicopter at an altitude of 150 feet. This photo includes the area marked off in Figure 1, and is also diagrammed in Figure 4. The average distance between individual buttresses in the lower middle of the Figure is from 9 to 12 meters, and the development of a dendritic drainage pattern of sediment from the lower *palmata* zone into deeper water is evident. The horizontal distance through the center of this airphoto is about 200 meters.

the falling of the wind. At such times water circulation on the reef becomes dependent on the ebb and flow of the tides.

The zonal structure of the reef becomes apparent by taking a profile traverse across it from shore to deep water. The different zones and regions are named according to their most conspicuous faunal or topographical characteristic. Their relationship to each other and to the reef as a whole is summarized in Table II. The appearance of this reef as a whole is seen in Figure 2 which is a vertical air photo taken from an altitude of 6,000 feet. Figure 3 is an oblique airphoto taken at an altitude of 150 feet from a helicopter. An enlarged portion of this is shown in Figure 4 while Figure 5 is an elevation view of the same area to demonstrate the cross sectional topography in detail.

Exact figures relating to the abundance or biomass of any given coral species per unit area in the different zones of the reef are not yet available. However, as a result of notes and observations during numerous transects that were made in this area, a rough approximation of the relative abundance of the different species could be obtained. This information is summarized in Table III to show the distributional pattern of corals on the reef. The number of plus signs following the species names is intended only as an indication of their relative abundance. The data are based on the relative frequency with which different scleractinian species were observed in the

TABLE II. Relationship of zones in a reef at Ocho Rios, Jamaica

Region	Zone		Average Width (meters)	Average Depth (meters)
Back-reef region	Shore zone		1- 10	0.5- 3
	Lagoon or channel		10-300	2 -15
Reef crest	Rear zone		3- 10	1 - 3
	Reef flat		20- 50	0.5- 3
	Palmata zone	Upper (breaker)	6- 10	0.5- 3
		Lower	30- 50	3 - 6
	Buttress zone		40- 60	1 -10
Seaward slope or fore-reef	*Cervicornis* zone		30- 60	7 -15
	Annularis zone		>60	15

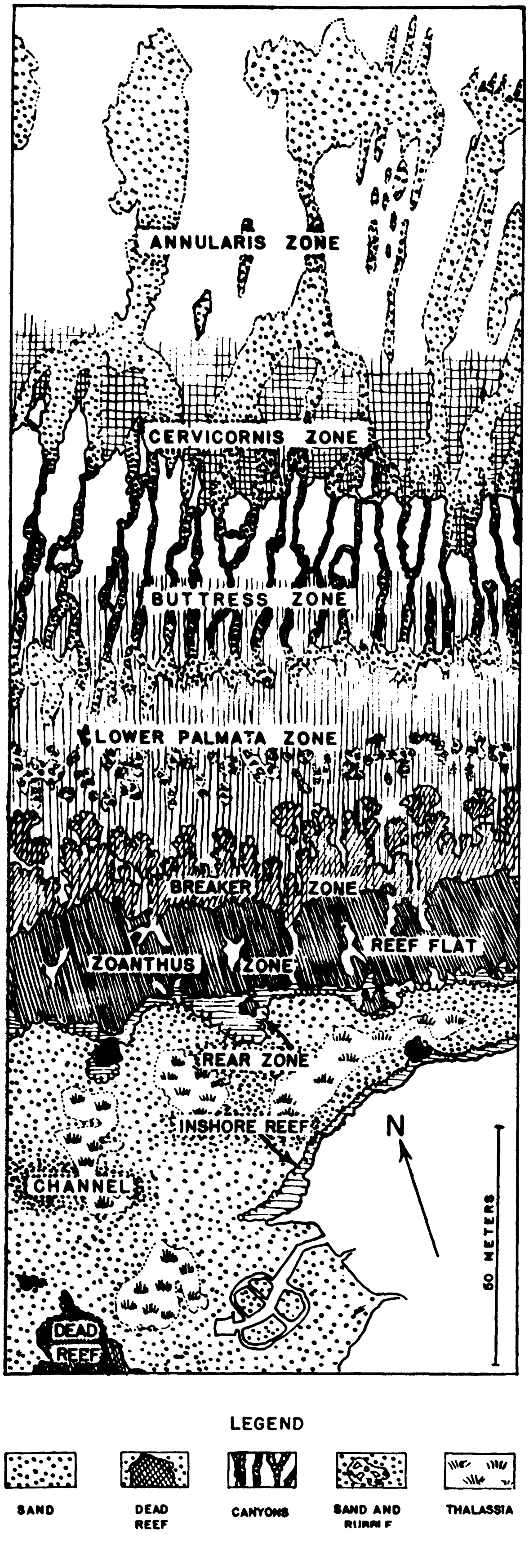

Fig. 4. Enlarged section of the reef in Figure 2 to show the succession of zones in greater detail. The shoreline is on the lower right and the seaward slope is at the top of the figure. The relationship of the buttress zone is clearly shown.

various zones at the time these transects were made. A quantitative survey of this reef is now in progress and will be reported in a subsequent paper.

Although this study is concerned essentially only with the reef building corals, some non-reef building, or ahermatypic, species are often found underneath large colonies, in tunnels and caverns within the reef, or in certain turbid harbour localities where the oxygen content of the water is reduced. These corals may become quite numerous in certain restricted areas but their abundance in terms of aggregate biomass is nevertheless only a very small fraction of that of the hermatypic corals.

The shore zone

A mixed and frequently rich scleractinian population is often observed on rocky shores at depths up to 3 meters. The most numerous species are *Acropora palmata, Montastrea annularis, M. cavernosa, Diploria strigosa, Porites astreoides, P. porites, Siderastrea siderea* and *Manicina areolata* (on sandy bottom). Encrusting *Lithothamnion* is usually abundant on exposed wave swept rocks. Hardy species such as *Diploria clivosa, Siderastrea radians* and *Favia fragum* occur where the inshore environment is turbid and sometimes stagnant.

The channel or lagoon zone

This region is between 10 and 300 meters wide and from 2 to 15 meters deep. The bottom is sandy and there is a correspondingly sparse coral population. Gorgonians, molluscs and echinoderms occur in large numbers but the bulk of the bottom sediments of this zone are formed from foraminifera and *Halimeda* fragments, with corals contributing comparatively little. Calcareous muds often occur in depressions and stagnant inlets. Large parts of the lagoon bottom are overgrown by strips of turtle grass (*Thalassia testudinum*) in which are often found small unattached colonies of *Manicina areolata* and *Porites divaricata*. In deeper parts of the lagoon there are isolated heads of *Montastrea annularis* and hillocks formed of *Porites porites* which may reach a height of several meters.

The rear zone

This region forms the inshore limit of the reef crest. It rises abruptly from the sandy bottom of the lagoon at a depth of 2 or 3 meters and is

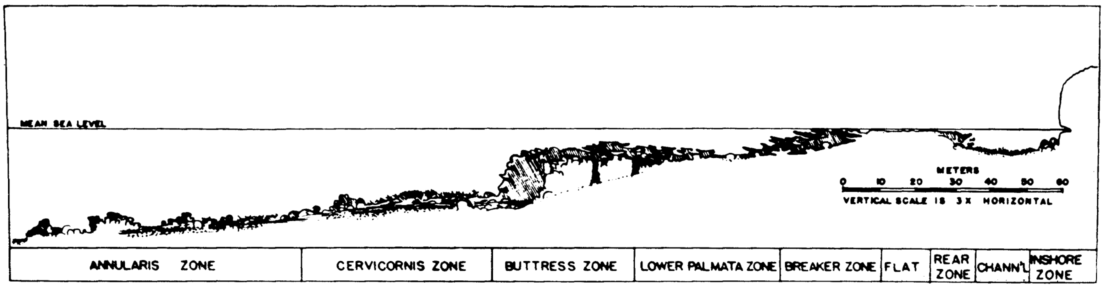

FIG. 5. Elevation view of a reef transect taken in a line coinciding approximately with a line drawn through the center of the reef area shown in Figure 2. The precipitous topography of the buttress zone is clearly indicated.

FIG. 6. Low altitude airphoto of the breaker zone and reef flat of the Ocho Rios reef taken with polaroid filter and extreme wide-angle lens from a helicopter. This shows the strongly oriented growth pattern of the *Acropora palmata* population in this regtion. It should be noted that this directional pattern is still preserved in the *Zonathus* overgrown reef flat in the upper middle of this figure, showing that the killed colonies have been incorporated *in situ* into the reef flat. The horizontal distance through the center of the figure is about 60 meters.

the site of a rich and varied coral population growing almost to the surface. The massive species predominate, among them *Montastrea annularis, Diploria strigosa, Montastrea cavernosa, Siderastrea siderea* and *Porites astreoides* are the most important. Branching species such as *Acropora palmata, A. cervicornis, A. prolifera, Porites porites* and *P. furcata* are also very common though less important in regard to their biomass.

The reef flat, or Zoanthus *zone*

This is the crest of the reef which is formed almost entirely from the dead and unconsolidated colonies of *Acropora palmata* (see Figures 6 and 7). Much of this has become overgrown with a thick rubbery mat of the green colonial zoanthid *Zoanthus sociatus* which gives this region of the Ocho Rios reef its characteristic appearance. Except for a few encrusting colonies of *Diploria clivosa,* corals are scarce on the reef flat but *Millepora, Gorgonia, Lithothamnion* and *Halimeda* are fairly abundant. A rich coral fauna, resembling that of the rear zone, is found in many of the shallow channels which cross this region. In some cases, lateral coral growth blocks the channels re-

TABLE III. Distribution of Shallow water Scleractinia on the Ocho Rios Reef*

Family and Species	Tide Pools	Back Reef		Reef Crest					Seaward Slope	
						Palmata Zone				
		Inshore Zone	Channel or Lagoon	Rear Zone	Reef Flat	Upper (Breaker)	Lower	Buttress Zone	Cervicornis Zone	Annularis Zone
ASTROCOENIIDAE										
S. michelinii			+	++						++
ACROPORIDAE										
A. cervicornis		++	+++	+++	+	+	+++	+++	++++++++++++	++++
A. palmata		+++++	+++	++++	+++	++++++++++++	+++++++	+++++++	+	
A. prolifera		++	+	+++	+	+	++	++	+++	++
POCILLOPORIDAE										
M. decactis			+					++	+	
M. asperula								++	+++	++++
AGARICIIDAE										
A. agaricites	+	++	+	++	++	+++	+++	+++++++++	+++	++
A. fragilis		+	+	+	+	+	+	+++	+	++
A. nobilis								+		
SIDERASTREIDAE										
S. radians	++++	+++	+++	++	++++	++	++	+		
S. siderea		+++	++++	++++	+	+	++	+++	++	+++
PORITIDAE										
P. astreoides	+	+++	++	+++	+++	+	+	++++++++	++	++++
P. porites		++	+++	++	+	+	++	+++	+++++++++	++++++
P. furcata		+	+	++				+++++	+++	+
P. divaricata			++	+						
FAVIIDAE										
F. fragum	++	+++	++	++	+++	+	+	+	+	
D. clivosa	++++	++++	+++	+++	+++	++	+			
D. strigosa		+++++	+++	+++++	++	++++	+++	++++	++	+++++
D. labyrinthiformis		+	+	+	+	++	++	+++	+	+++++
C. amaranthus							+	+	+	++
C. natans		+	+++	+	+	+	++	+++++	++++	+++++
M. areolata		++	+++	+			+			
C. arbuscula			+							
M. annularis		++	+++	++++	+	+	+	++++++++++++	+++++++	++++++++++++
M. cavernosa		+++	+++	+++	+		+	+	+	++
RHIZANGIIDAE										
P. americana		+	+							
A. solitaria		+	+	+			+	+	+	+
OCULINIDAE										
O. diffusa		+	+							+
O. valenciennesi										+?
MEANDRINIDAE										
M. meandrites		+	+					+	+	++
M. braziliensis										++?
D. stokesi		++	+	++	+		+	+	+	+
D. cylindrus				+	+		+	+	+	+
MUSSIDAE										
M. angulosa				+			+	++	+	++
I. rigida		+	+	+			++	+	+	+
I. multiflora		+	+	+				+	+	+
I. sinuosa		++	++	++			+	+		
M. lamarckana		+		+			+	++	+	+
CARYOPHYLLIIDAE										
E. fastigiata		++	+	+			+	+	+	++
DENDROPHYLLIIDAE										
T. tenuilamellosa		+						+		
MILLEPORINA										
M. alcicornis		++	+	+	+++	++++	+++++	++++++	+++	+
STYLASTERINA										
Stylaster sp.								+	+	+

*The number of plus signs following the species names in this table is not to be interpreted as having quantitative connotations other than that it corresponds to averages of rough species counts made on this reef during repeated traverses. Arbitrarily, 1 plus can be taken to mean rare; 2 plus is scarce; 3-4 plus is common; 5-7 plus is abundant and 8-12 plus is very abundant.

sulting in the formation of isolated pools. This zone is on the average 40 meters wide and less than half a meter deep except in the channels and pools where the depth may increase to over 2 meters.

The palmata zone

In the upper, or breaker, region of this zone, the *Zoanthus* overgrown reef flat abruptly gives way to a narrow zone which is populated almost exclusively by huge tree-like colonies of *Acropora*

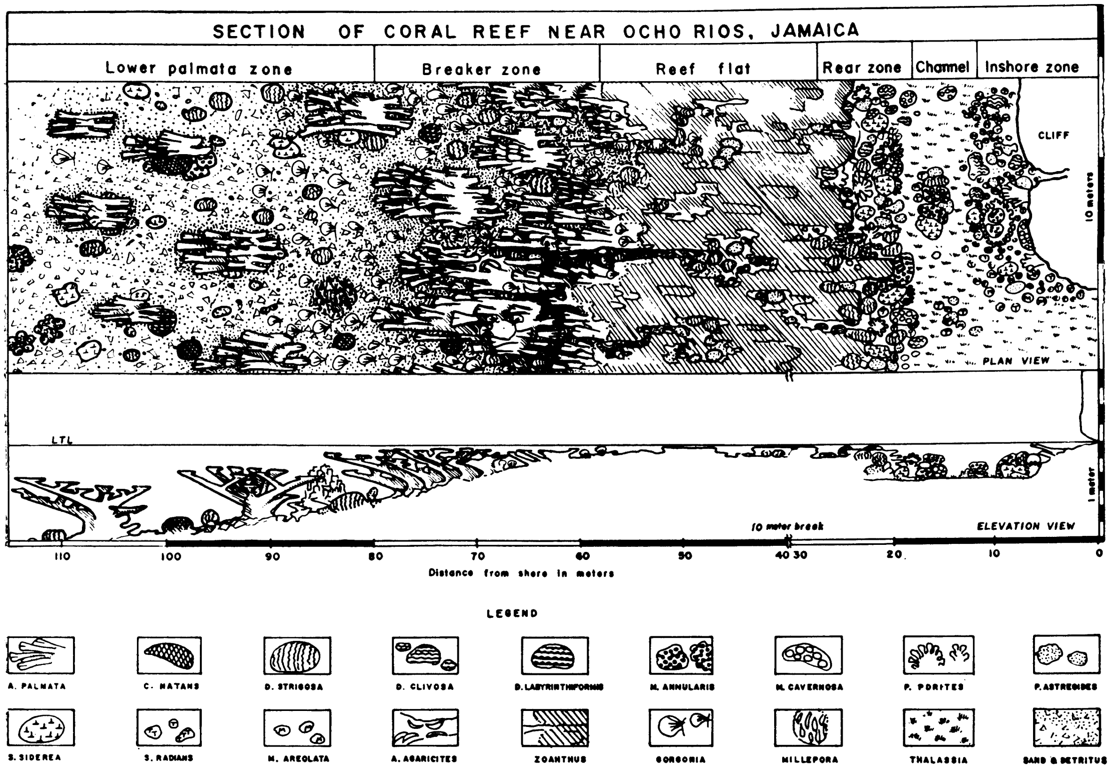

FIG. 7. Detailed plan view of the crest and back reef zones of the Ocho Rios reef to show the distribution pattern of individual coral colonies in this region. The size of individual corals is exaggerated about 4 times and the actual number of colonies is therefore reduced by a proportional amount. The shoreline is on the right hand side of the figure.

palmata that take the full force of the surf. The great serried outliers of this coral are predominantly oriented in the direction of the prevailing seas which thus give the whole zone the characteristic appearance of a great jagged comb with irregular teeth. This can be seen in Figures 6, 7 and 8. In this region, *Acropora palmata* is clearly dominant and exists as a nearly pure population except on the sides of surge channels where *Diploria strigosa, Porites astreoides, Agaricia agaricites* and other corals may be found in some numbers. *Millepora alcicornis* often forms great heads which, like *Acropora,* take the full force of the surf. *Gorgonia* and *Lithothamnion* are common on dead coral, and the bottom is in many places littered with broken, dead and overturned colonies of *Acropora palmata.*

In front of the breaker zone, the reef slopes gently downward to depths of between 5 and 6 meters over a distance of from 30 to 60 meters. This lower *palmata* region forms a kind of moat since the reef becomes shallower again in the buttress zone which is the next zone to the seaward (see Figure 4). *Acropora palmata* is still the dominant coral, growing in large isolated heads that also are strongly oriented into the prevailing seas. The density of living coral is much reduced in comparison to the breaker zone, and large areas of the bottom are covered with unconsolidated rubble on which coral growth is sparse.

The deeper parts of this zone have a more diverse coral population, consisting of *Diploria strigosa, Montastrea annularis, Acropora cervicornis, Colpophyllia natans, Porites astreoides, P. porites, P. furcata, Agaricia agaricites,* mussids, and *Millepora* scattered among some larger heads of *Acropora palmata.* Foraminifera together with *Halimeda* and other calcareous algae are abundant, forming more than 60% of the bulk of the finer sediments.

The buttress zone

Along the greater part of the reef, the lower *palmata* zone merges abruptly into a region of spectacular underwater scenery. The most remarkable features of this zone are huge spurs or buttresses of living coral which project outward into much deeper water. These are separated from each other by a series of very narrow, somewhat winding, canyons the walls of which are perpendicular or even overhanging. This can be

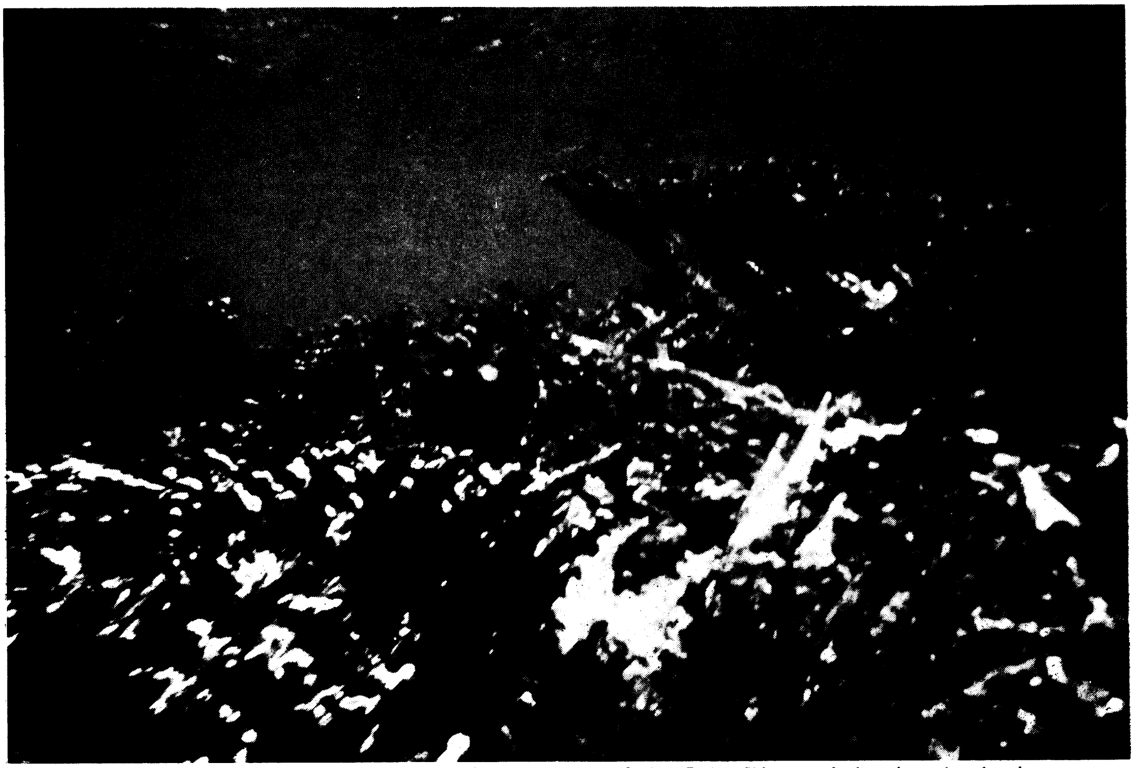

FIG. 8. Underwater view of coral in the breaker zone of the Ocho Rios reef showing the dominant population of *Acropora palmata* that is characteristic of this region. The top of the coral outlier on the right of the figure is only a half a meter below the water surface. A large still living colony which has been tilted on its side can be seen on the left, and some killed and partly broken up *A. palmata* is shown in the center. The depth here is about 3 meters and the horizontal distance through the center of the figure is about 15 meters.

seen in the underwater photograph in Figure 9. The buttresses and canyons run roughly parallel to each other in a direction that is always normal to the reef front. At the buttress crests, the depth averages only about 2 meters whereas the canyons are between 8 and 10 meters deep.

The alternation of buttress with canyon on the Ocho Rios reef is surprisingly uniform over considerable distances. Large scale aerial survey photographs show that this zone extends, with a few interruptions, along the north coast from Port Antonio in the east to Montego Bay in the west, a distance of about 130 miles. An example of the topography of this zone is given in figure 10 which shows the results of a series of cross sectional and longitudinal transects in the buttress zone of the reef opposite "Sombra," near Ocho Rios. In this region, the crest-to-crest distance between the coral spurs averages 8 meters, the width of the canyons being between one and 2 meters, but in some cases they were seen to be as wide as 10 meters or more. More recently, however, we have seen from the air considerably larger buttresses and much deeper canyons in the reef area between Oracabessa and Salt Gut some 10 miles east of Ocho Rios such as are shown in Figure 11. There appears to be considerable local variation in the degree of development of this zone although the overall characteristics described in this paper seem to apply in all those areas which we have so far explored.

The spurs of the buttresses usually terminate abruptly to form a steep promontory jutting out into deeper water, as shown in Figure 12. The canyons, on the other hand, continue outward across the fore reef as strips of sand for distances of several hundred meters. The buttress zone is by far the richest in the reef from the point of view of biomass of living coral per unit area. More than 90% of the available surface is covered by living coral, the exception being the narrow sand strips at the bottom of the canyons from which coral is usually absent.

Along the greater part of the reef, the buttresses support a large population of *Agaricia agaricites,* this being the only region where this species may become co-dominant as seen in Figure 13. The extreme hardness and toughness of this coral probably accounts to some extent for the resistance of the buttresses to storm damage. Also abundant on the spur crests are large tree-like growths of *Acropora palmata,* great multilobar

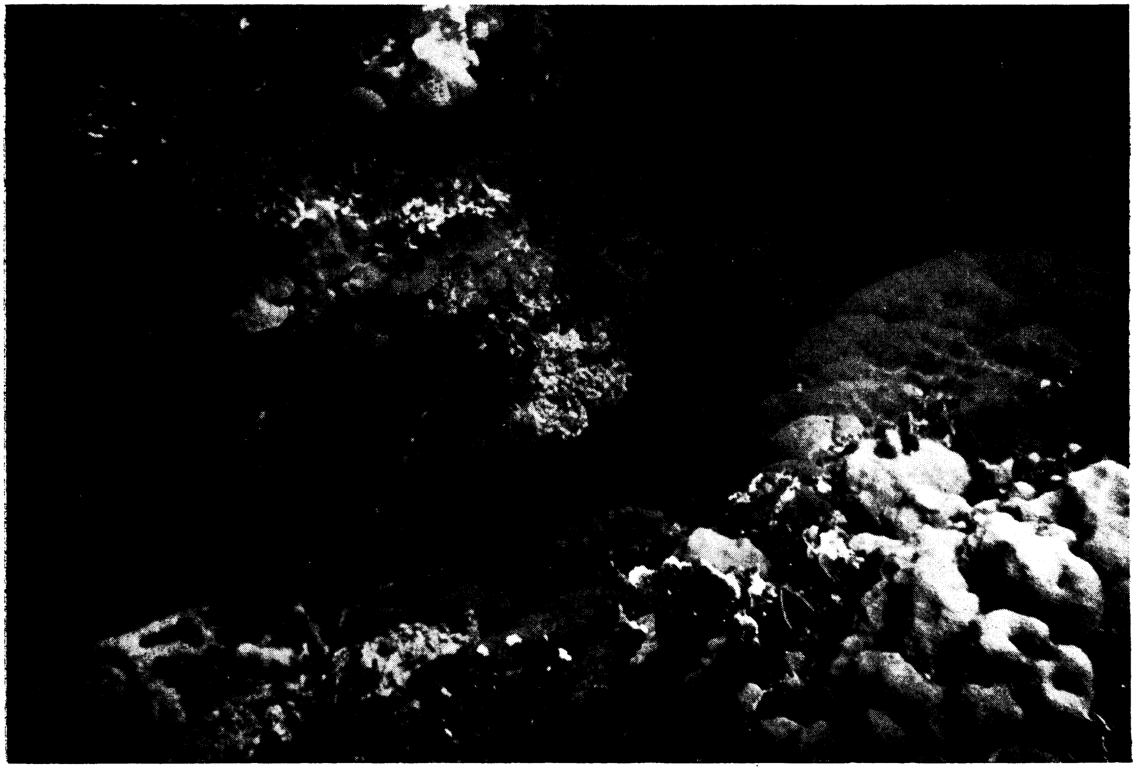

FIG. 9. Vertical underwater view into a canyon between 2 buttresses in the Ocho Rios reef. The walls which are nearly perpendicular are formed predominantly of large massive colonies of *Montastrea annularis* some of which are shown on the lower right canyon wall. The shingle-like colonies seen on the upper left hand side are *Porites astreoides,* an important secondary hermatype in this zone. The canyon bottom lies about 8 meters beneath the surface and is covered by sand showing ripple marks. The narrowest part of the canyon is less than one meter wide. The horizontal distance through the center of the figure is about 8 meters.

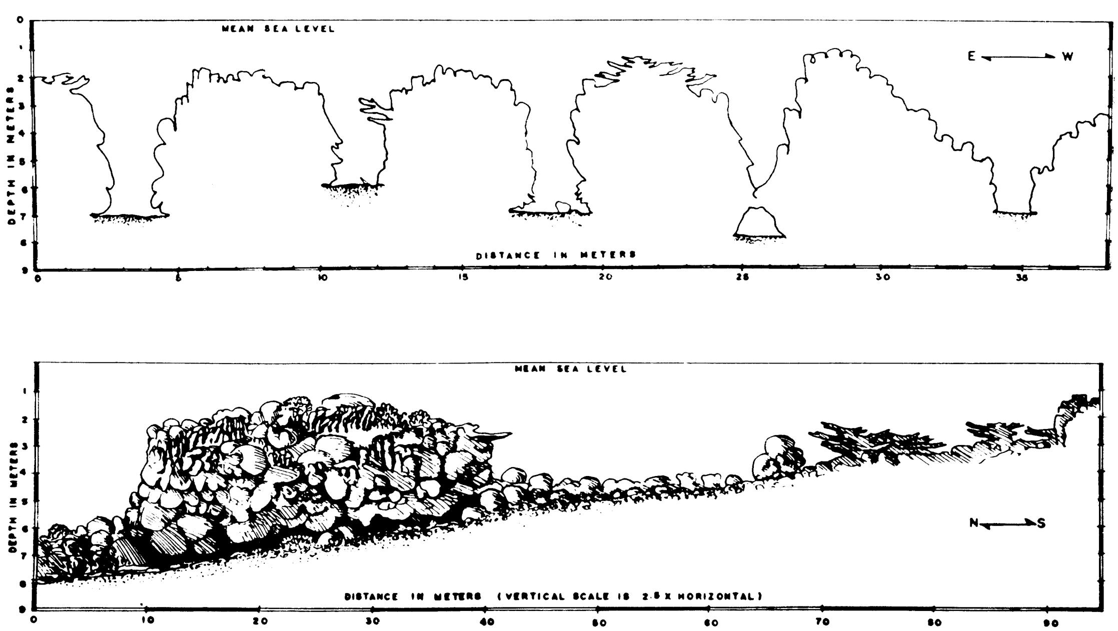

FIGURE 10. Cross sectional and longitudinal transects of the buttress zone in the reef near "Sombra," Ocho Rios. Depths and horizontal distances along the traverse were measured with a sounding line and details filled in from underwater photographs and field sketches. Vigorous growth of coral in the buttresses has resulted in a sharp elevation of these structures above the surrounding sea bottom.

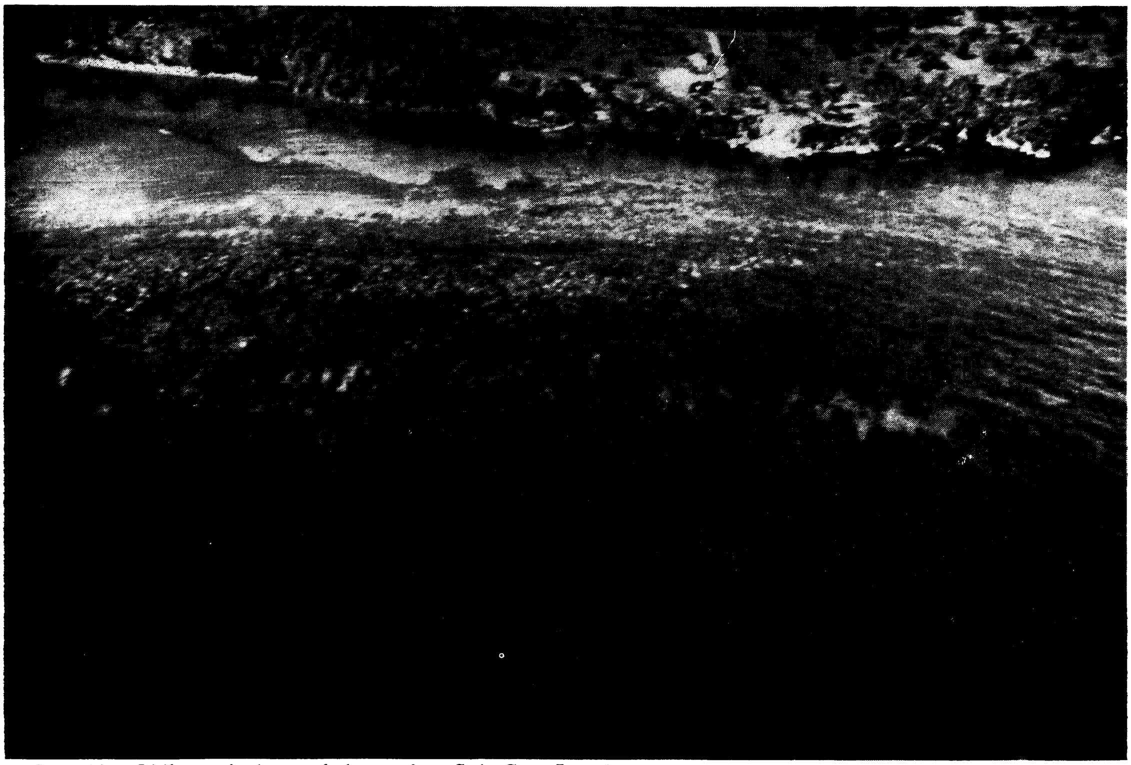

FIG. 11. Oblique airphoto of the reef at Salt Gut, Jamaica, taken with polaroid filter and extreme wide angle lens from a helicopter at an altitude of about 125 feet. In this reef the buttresses are several times larger than they are at Ocho Rios, 10 miles to the west, and the maximum depth of the canyons appears to be about 20 meters. The horizontal distance through the center of the figure is about 200 meters.

heads of *Montastrea annularis, Millepora, Porites porites* and *P. furcata,* and in some places, *Acropora cervicornis* and *A. prolifera.*

The buttress sides are built up primarily by gigantic colonies of *Montastrea annularis* which assume the curious flattened habit shown in the underwater photographs in Figures 14 and 15. *Porites astreoides* is also very common and grows in flattened plate-like colonies the edges of which overlap, giving an appearance of shingles on a roof. Very large colonies of *Colpophyllia natans, Diploria strigosa, D. labyrinthiformis,* and *Dendrogyra cylindrus* are also fairly common (Figure 16). The prevalent zoanthidean in this zone is *Palythoa caribbaea.* Corals which are rare elsewhere on the reef, such as *Madracis asperula, M. decactis, Mycetophyllia lamarckana, Mussa angulosa* and others, become numerous in this zone though they remain unimportant from the point of view of their biomass.

The cervicornis *zone*

The uppermost region of the seaward slope of the fore reef takes its name from the immense beds of staghorn coral, *Acropora cervicornis,* which occur here. The zone is from 30 to 100 meters wide and between 8 and 15 meters deep. It is transected by elongated sandy tracts which are the outward continuations of some of the canyons. The bottom tends to be uneven due to extensive coral growth between the sandy areas. Large colonies of *Montastrea annularis, Porites porites* and *P. furcata* are also abundant, and it is the growth of these corals which appears to initiate the formation of the buttresses in the deeper zones of the seaward slope as seen in Figure 17.

The annularis *zone*

This is the deepest part of the fore reef so far explored. It is characterized by great numbers of multilobar heads of *Montastrea annularis.* Other species as *Diploria labyrinthiformis, D. strigosa, Colpophyllia natans, C. amaranthus, Siderastrea siderea, Porites astreoides, P. porites, Meandrina meandrites, Dendrogyra cylindrus, Dichocoenia stokesii* and various mussids are also more or less abundant and combine to form a rich mixed bottom community. Except for small patches of *Acropora cervicornis,* the Acroporidae are inconspicuous or indeed absent at depths greater than about 15 meters on Jamaican reefs.

Less than 50% of the bottom area of this zone is covered by living coral, and growth is much less vigorous than in the upper zones of the reef.

FIG. 12. Underwater view of the seaward termination of a buttress in the Ocho Rios reef, showing a steep promontory projecting outward into much deeper water. The top of this buttress lies 2 meters beneath the surface, the bottom beyond is more than 10 meters deep. The buttress crest bears a large colony of *Porites furcata,* the large coral knobs are ***Montastrea annularis.*** The flattened growths on the buttress sides are *Millepora alcicornis* and the circular plate-like colonies are *Porites astreoides.* The vertical distance in the middle of the figure is about 6 meters.

It is the writer's impression that both the number and size of the coral colonies per unit area decreases below depths of 20 meters, but this observation must be tentative until more information is available about the deeper regions of the seaward slope.

Zonation in the Port Royal Reefs

The type of zonation described in the preceding section applies in principle to all Jamaican climax reef communities despite the fact that there is considerable variation in the degree of development of the zones in different localities. On the south coast of Jamaica, the largest reefs are to be found between Port Royal and Portland Point. Smaller reefs also exist near the eastern and western ends of the island, and scattered coral growth is frequently found on the bottom even where no true reef communities have become established. Eroded remains of what may once have been extensive reefs can be seen near Morant Bay, Black River and Alligator Pond. Some of these reefs may have been buried by shifting sands and subsequently re-exposed.

Many of the large south-coast reefs in Jamaica show evidence of regression in recent times and there is every indication that the population density in terms of biomass of coral per unit area is lower here than on comparable reefs on the north coast. The most important attributes in which the larger outer reefs near Port Royal differ from the reef at Ocho Rios are: (1) total absence of a buttress zone; (2) very large areas of dead coral in the upper *palmata* zone; (3) a lower population density of acroporid corals in the breaker zone, and (4) the reef crest is more trenched and usually covered with living coral from which *Zoanthus* is practically absent.

It is probable that at least some of these differences are due to the destruction wrought by hurricanes, the most recent of which devastated the southeastern coast of Jamaica in August 1951. The effects of such storms on the population structure of a reef will be discussed below.

The lagoon

South of Port Royal, an area of the shallow offshore shelf about 5 miles wide by 8 miles long

FIG. 13. Underwater view of the landward termination of a large buttress in the Ocho Rios reef, looking backward at the lower *palmata* zone. The height of the buttress wall on the right of the figure is about 4 meters. In the left foreground are some typical mammellate growths of *Montastrea annularis* whereas on the right, this same species shows a flattened colony habit that is characteristic of it when growing on a near vertical surface. The canyon opening out in the middle foreground is partly filled with living coral and detritus, and in the background is a large coral head about 5 meters high composed primarily of *Acropora cervicornis* and crowned with large colonies of *A. palmata*.

has been more or less enclosed by a series of patch and barrier reefs together with their associated cays. The resulting lagoon has an uneven bottom with depths as great as 35 meters and many coral hillocks rising almost to the surface. In its deeper parts, the lagoon floor is covered mostly by calcareous sediments on which living coral growth is incidental or absent.

The large sand and rubble shallows on the western (lee) sides of the cays, are often overgrown with *Thalassia* and *Halimeda*. Here, the small scleractinians such as *Manicina areolata, Porites divericata,* and *Cladocaroa arbuscula* are very common. In somewhat deeper waters, up to 3 meters, *Acropora palmata, Montastrea annularis, M. cavernosa, Porites astreoides, Diploria clivosa, D. strigosa,* and *Acropora cervicornis* and gorgonians are common but they have a patchy distribution. At greater depths, the most important scleractinian is *Montastrea annularis* which forms great multilobar heads that remain separate from each other and show little tendency to aggregate into reefs. In some areas, the bottom is covered with dense growths of *Acropora cervicornis.* The bulk of the fined sediment is made up of *Halimeda* and foraminiferan fragments. The delicate branching coral *Oculina diffusa* is common in the western part of the lagoon where outflowing Kingston Harbour water and muddy bottom provides a somewhat different environment from that found on the reefs.

The reef crest

The barrier reef between South Cay and Southeast Cay, near Port Royal, is about 4 miles long with a crest about 30 meters wide. The maximum depth of the narrow interconnecting channels which cross the area is about a meter and a half, but the tops of the coral colonies are often awash. See Figure 18. In appearance and coral population this region closely resembles the rear zone of the Ocho Rios reef. There is a rich mixed community in which the most prevalent species are *Diploria strigosa, D. clivosa, Montastrea annularis, Porites astreoides, P. porites, Siderastrea siderea, Acropora palmata* and *A. cervicornis,* The Zoanthidea are represented by *Palythoa,* rather than *Zoanthus* which is not common. *Mille-*

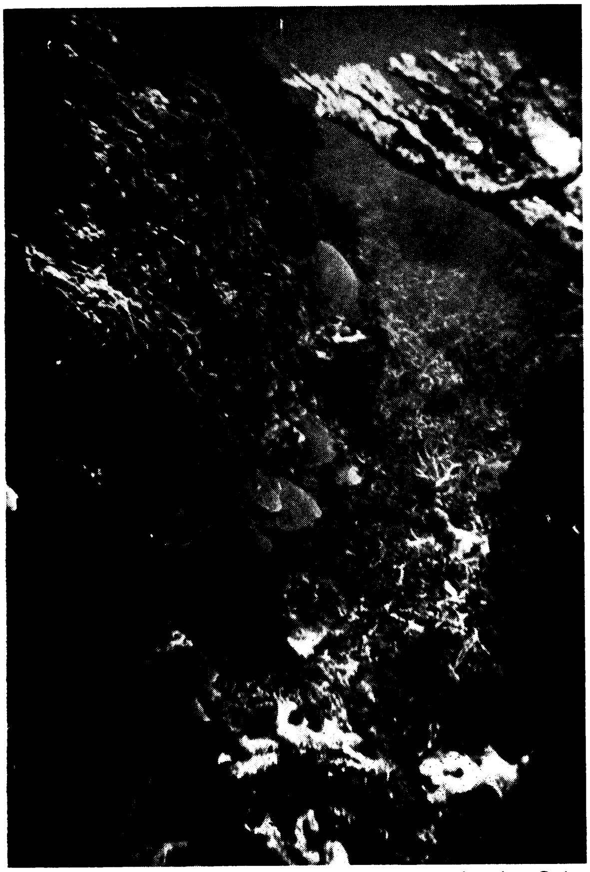

FIG. 14. Underwater view of a canyon in the Ocho Rios reef showing the buttress wall covered by very large colonies of *Agaricia agaricites*. This view is in a seaward direction, looking out over the *cervicornis* zone. The canyon shows evidence of being partly filled in through accumulation of coral detritus composed mostly of fragmented *A. palmata* (lower foreground), *A. cervicornis* and *Porites furcata*. Depth of photo is about 4 meters.

pora alcicornis exists in this zone as rather small encrusting colonies. In many places the reef crest is replaced by shingle ramparts which in some cases have grown large enough to form islands or cays able to support land plants such as Mangrove, *Ipomea* and *Sesuvium*. There is no well defined rear zone; instead, the reef crest merges gradually with the lagoon and the number of corals becomes progressively smaller until only a few hardy specimens of *Porites astreoides*, *Diploria clivosa*, *Favia fragum* and *Siderastrea radians* remain in the shallow sand flats.

The breaker zone

The breaker zone of the main barrier reef that forms the southern boundary of the Port Royal tract has an atypical appearance because the elkhorn coral *Acropora palmata* does not achieve the spectacular growth that is so characteristic of it on the north coast reefs. This zone is in many places severely damaged and the bottom is strewn with dead, broken and and overturned colonies, as seen in Figure 19. *Acropora palmata* is still very common, but it no longer enjoys the dominant position that it does on other reefs. To some extent it has been replaced by *Diploria strigosa*, a massive "brain coral" which grows to very large sizes here (see Figure 20). *Millepora* is another hermatype which has taken advantage of the lack of competition. This is more abundant than *Acropora palmata* in many localities, and forms great flattened heads about 5 meters long and 4 high, as shown in Figure 21. The tops of these formations are usually awash and often exposed at low tide. In many cases the uppermost parts of these heads are dead and overgrown by a veneer of *Lithothamnion*. On the eastern windward sides of Southeast Cay, Maiden Cay and Gun Cay, large groups of *Millepora* colonies coalesce to form true hydrozoan reefs.

As a result of these observations we believe that the somewhat anomalous population structure of this reef zone may be due to disruption of normal reef growth processes by severe storms, or, less likely, by the great earthquakes which destroyed nearby Port Royal in 1692 and Kingston in 1907. Whatever the cause, the presence of enormous amounts of *Acropora palmata* shingle, together with the fact that there is a comparatively reduced population of living acroporids over large parts of this zone at the present time, may be taken as evidence that this reef has been more productive in the recent past.

The seaward slope

In these reefs, which lack the buttress zone, the *palmata* zone is part of the fore reef. As indicated by the great masses of *Acropora* rubble which cover about 80% of the bottom, there has been severe damage and little living coral remains down to depths of approximately 6 meters. However, in isolated localities, where the coral has escaped destruction, the normal ecological structure of the reef is preserved and there are very rich populations of *Acropora palmata* which resemble those seen on the north coast. Other cases of extensive coral destruction have been noted by Steers *et al.* (1940) on several days in Portland Bight, and by Zans (1957b) on the Pedro Cays. The recolonization of the denuded areas by coral seems to be slow, presumably due to the instability of the unconsolidated shingle Hence much of this region is a submarine desert in comparison to the corresponding zone of the Ocho Rios reef.

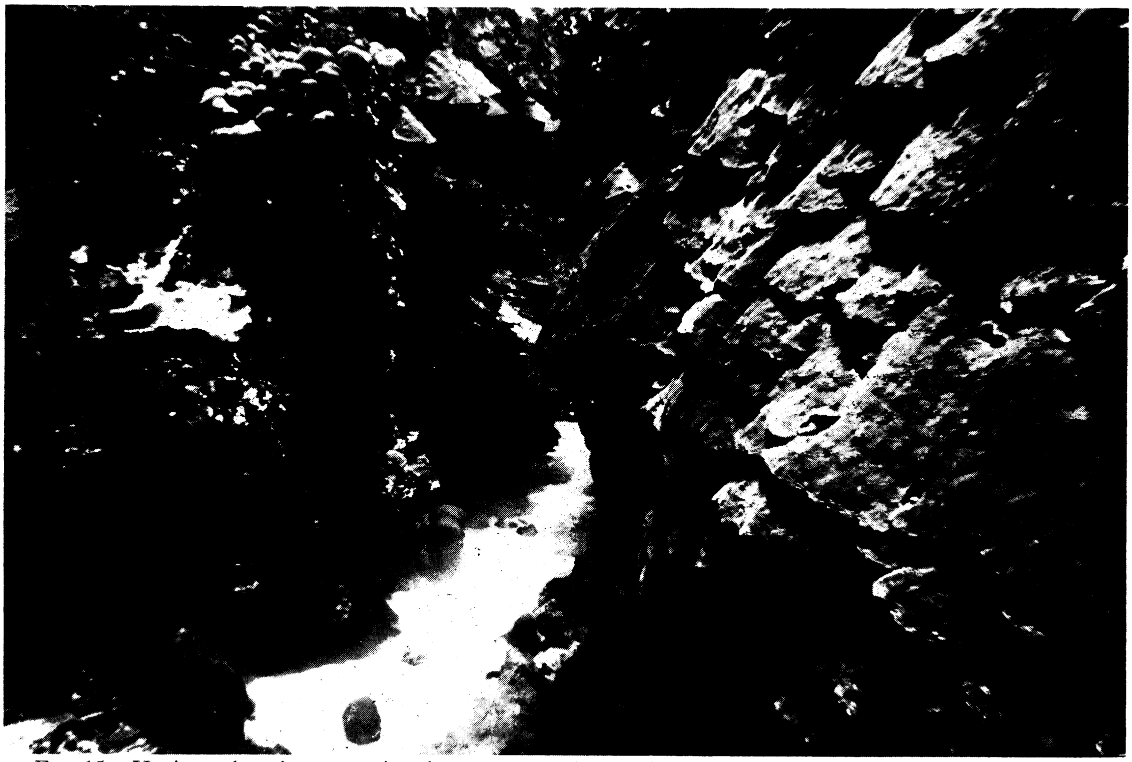

FIG. 15. Horizontal underwater view into a canyon in the Ocho Rios reef. The depth at which the photo was taken is about 9 meters. Here the canyon is floored by fine sand. The buttress wall on the right is composed of a single gigantic colony of *Montastrea annularis* which has assumed a flattened shingle-like habit, resembling flow sheets. The vertical distance covered by the middle of the figure is about 4 meters.

The deeper parts of the fore reef have typical *cervicornis* and *annularis* zones which differ from those on the north coast only in that there is rather less vigorous growth of coral and larger sandy areas which contain no coral at all.

DISCUSSION

The distribution of shallow water Scleractinia in the Caribbean area

The Caribbean area is remarkably homogeneous with regard to the shallow-water Scleractinia. There are no important regional differences in the reef coral populations and no corals have yet been found that are peculiar to any one locality. Even in the case of Bermuda, which lacks four families and twelve species, there are no shallow-water corals which are not commonly found elsewhere in the Caribbean area. This fact is demonstrated in Table IV which compares the known scleractinian fauna of Jamaica (41 species) with that of Florida (42 species), Bahamas (37 species), Barbados (26 species) and Bermuda (19 species). The variation of the species number in the first three localities is almost certainly due to the vagaries of "collector's luck" rather than to any significant faunistic differences, whereas the list of Barbadian species is probably still incomplete and no conclusions can be drawn. Bermuda, on the other hand, definitely lacks the Acroporidae, the Meandrinidae, the Dendrophylliidae and the Caryophylliidae, as well as many of the Faviidae, Poritidae and others.

Vaughan and Wells (1943 pp. 76-77) stated that the Bahamas had more species of hermatypic corals than any other locality in the West Indies. However, it is clear from more recent evidence (cf. Smith 1948, and this paper) that a species maximum may exist in that part of the Caribbean delineated roughly by Florida and the Bahamas in the north, the Isle of Pines in the west, and Jamaica and Puerto Rico in the south. However, far too little accurate information is at present available on the distribution of hermatypic corals in the West Indies to define with any exactitude the limits of such a coral population center. A careful survey is required in which special attention is paid to the peripheral islands, for example Anegada, Barbuda, Guadeloupe, Barbados, Tobago, Curacao and Bonaire, and to the reefs of the San Blas Archipelago in Panama, the Mosquito Cays near Nicaragua, Cozumel Island and Vera Cruz (see Heilprin 1890) in Mexico. Reliable check lists of the reef building corals should also

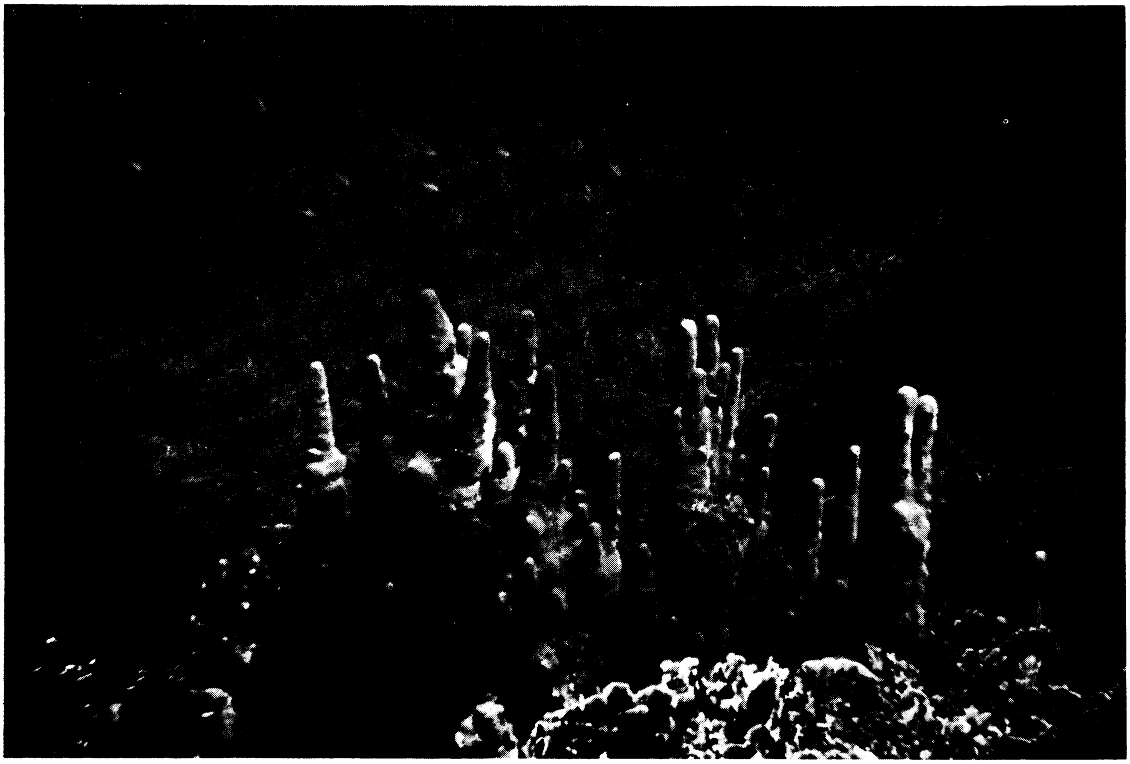

FIG. 16. Underwater view of the region where the buttress and *cervicornis* zones merge. The latter is seen in the background. In the foreground is a very large colony of *Dendrogyra cylindrus* growing at the outer foot of a buttress in the Ocho Rios reef. The depth of the great thicket of *Acropora cervicornis* in the background is about 10 meters.

be compiled for Cuba, Hispaniola, Puerto Rico, and the Virgin Islands. Thus, rather than to answer questions, the present study can only serve to point out the necessary steps to be taken in solving the problem of the origin and distribution of the Caribbean reef coral populations.

Growth and zonation of an offshore reef

The accumulation of calcareous matter by corals and other hermatypes to form a reef depends on 2 important factors. First, the overall rate of deposition must exceed the rate of erosion from all causes. Second, a suitable framework consisting of large coral or algal blocks must be formed in which finer detritus can accumulate and consolidate.

Given optimum conditions for growth the total transfer rate of calcium carbonate by hermatypes into the reef depends on the biomass of the various species, their growth rate, the resistance of their skeletons to erosion and translocation, and the speed with which the skeletal material is finally consolidated into the permanent structure of the reef. Whether a dead coral colony is buried *in situ* into the reef framework or whether it is first broken up, disintegrated and transported away to become a part of the unconsolidated sediments of the fore reef and lagoon is determined by such factors as the size and shape of the colony, *e.g.*, large or small, massive or branching, its hardness and the degree of exposure to heavy seas and other forms of mechanical or chemical attrition.

The question of whether there is a single most important coral species from the point of view the bulk of calcareous material it contributes to the framework of the reef is an interesting one. Ginsburg (1956) sums up the prevalent notion in his recent paper to the effect that elkhorn coral *Acropora palmata* is the primary structural element of Floridian reefs, providing a framework in which detrital material can accumulate.

Since the shallow zones of the reef described above are as a rule dominated by the great branching growths of *Acropora palmata,* and since fragmented colonies of this coral form the bulk of the calcareous detritus thrown up on the shingle ramparts, it is natural to conclude on the basis of superficial examination that this species might therefore also be the primary hermatype of Jamaican reefs. However, our observations on these reefs indicate that *Acropora palmata* is restricted almost entirely to the zones in the upper six

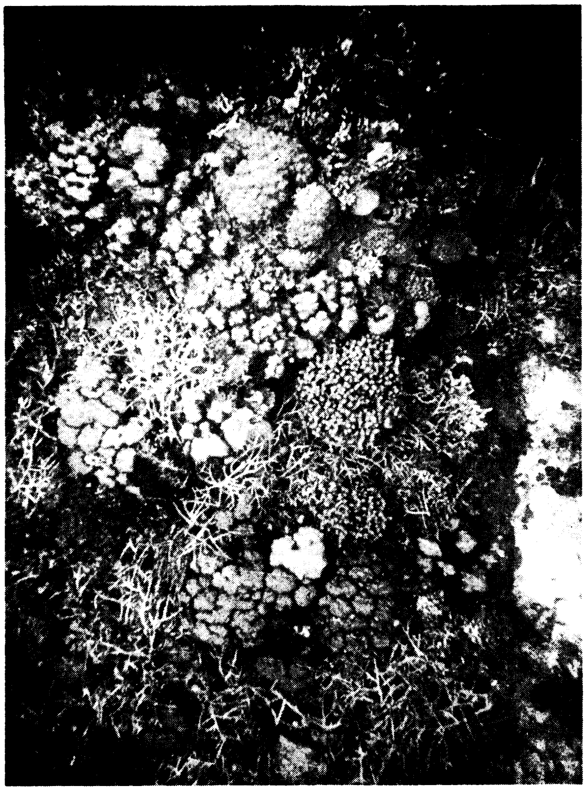

FIG. 17. Vertical underwater view of the junction between the buttress and *cervicornis* zones, showing the characteristically rich growth of coral in this region. The massive coral is *Montastrea annularis,* the blunt branched coral in the center is *Porites furcata.* A large bed of staghorn coral *A. cervicornis* grows in the space between the more massive corals. The *cervicornis* zone starts on the left of the figure. The sandy strip running across the bottom is a canyon debouching from the buttress zone. The depth is about 8 meters.

meters of the reef habitat, and that the most vigorous proliferation occurs not in the *palmata* zone but in the buttress zone where enormous colonies of *Montastrea annularis* make up the greater part of the calcareous material of which the reef is composed. It is interesting to note in this connection that *Montastrea* sp. is also by far the commonest and often the only fossil framework coral to be found in exposures of the Pliocene and more recent coastal reef limestones of northern Jamaica.

The extensive proliferation of *Acropora palmata* that is so characteristic of the upper zones of West Indian reefs probably indicates a reef community in the later stages of development. To provide the shallow conditions necessary for the growth of this coral however, a suitable platform must first be formed; in many cases this is accomplished by the activities of other coral species. In Jamaican reefs, the broad base of the reef is formed predominantly by *Montastrea annularis,* with such branching species as *Porites furcata* and

TABLE IV. Geographic distribution of West Indian shallow water corals*

Family and Species[1,2]	Jamaica[3,4,5]	Florida[6,7]	Bahamas[6,7]	Barbados[8,9,10]	Bermuda[7,11]
ASTROCOENIIDAE					
A. pectinata	−	+	−	−	−
S. michelinii	+	+	+	+	+
ACROPORIDAE					
A. cervicornis	+	+	+	+	−
A. palmata	+	+	+	+	−
A. prolifera	+	+	+	−	−
I OCILLOPORIDAE					
M. decactis	+	+	+	+	+
M. asperula	+	−	−	+	−
AGARICIIDAE					
A. agaricites	+	+	+	−	−
A. fragilis	+	+	−	+	+
A. nobilis	+	+	+	−	−
SIDERASTREIDAE					
S. radians	+	+	+	+	+
S. siderea	+	+	+	+	+
PORITIDAE					
P. astreoides	+	+	+	+	+
P. branneri	−	−	+	−	−
P. divaricata	+	+	−	−	−
P. furcata	+	+	+	−	−
P. porites	+	+	+	+	+
FAVIIDAE					
F. fragum	+	+	+	+	+
D. clivosa	+	+	+	+	−
D. strigcsa	+	+	+	+	+
D. labyrinthiformis	+	+	+	+	+
C. amaranthus	+	+	+	−	−
C. natans	+	+	+	+	−
M.areolata	+	+	+	−	−
M.mayori	−	+	−	−	−
C. arbuscula	+	+	+	−	−
S. bournoni	−	+	+	−	−
S. hyades	+	+	−	−	−
M. annularis	+	+	+	+	+
M. cavernosa	+	+	+	+	+
RHIZANGIIDAE					
A. solitaria	+	+	+	+	+
P. americana	+	+	−	−	−
OCULINIDAE					
O. diffusa	+	+	+	−	+
O. valenciennesi	+(?)	−	+	−	+
O. varicosa	−	+	−	+	+
MEANDRINIDAE					
M. meandrites	+	+	+	−	−
M. braziliensis	+	+	+	+	−
D. stokesi	+	+	+	+	−
D. cylindrus	+	+	+	+	−
MUSSIDAE					
M. angulosa	+	+	+	+	−
I. rigida	+	+	+	−	+
I. multiflora	+	+	+	+	+
I. sinuosa	+	+	+	−	+
M. lamarckana	+	+	+	+	−
CARYOPHYLLIIDAE					
E. fastigiata	+	+	+	+	−
DENDROPHYLLIIDAE					
T. tenuilamellosa	+	−	−	−	−
Total species	41	42	37	26	19

*[1]Vaughan and Wells (1943
[2]Wells (1956)
[3]Goreau (1956)
[4]Duerden (1902)
[5]Fontaine (1954)
[6]Vaughan (1910 et seq.)
[7]Smith (1948)
[8]Goreau (unpublished field notes)
[9]Butch (1939)
[10]Nutting (1919)
[11]Verrill (1901b)

Acropora cervicornis providing most of the finer detritus that fills the crevices between the colonies

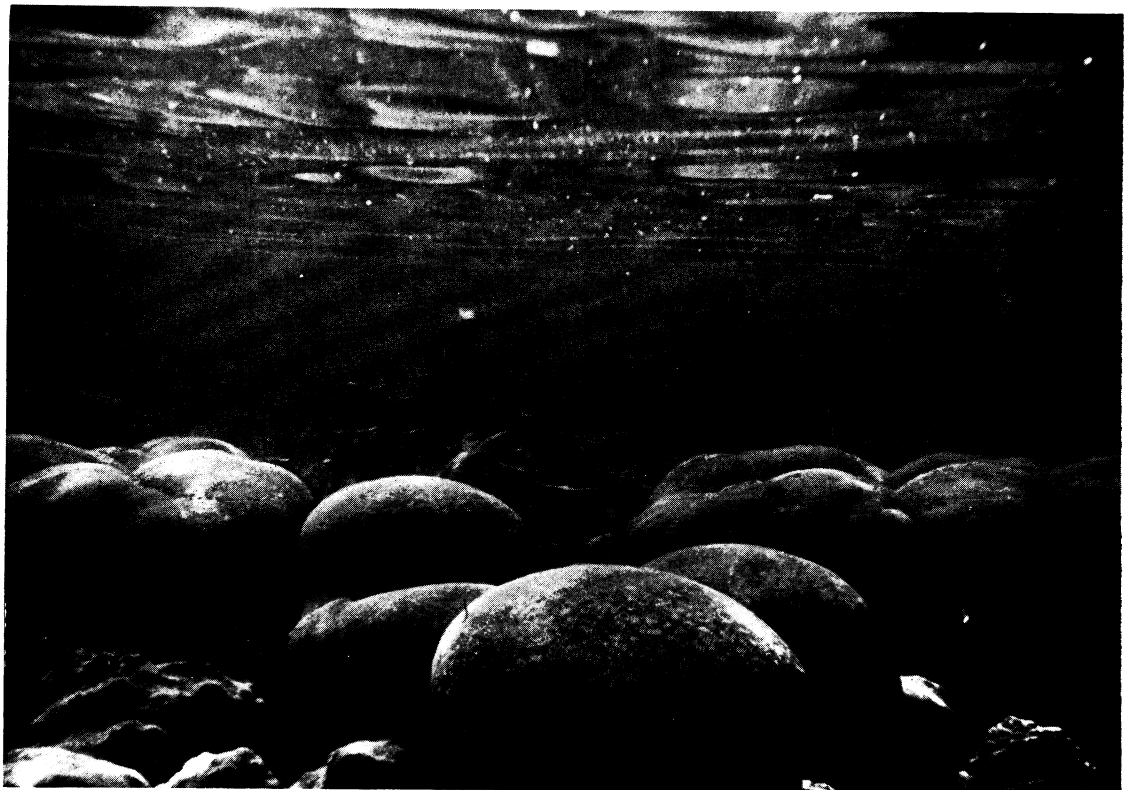

FIG. 18. Underwater view of the reef crest of the barrier reef near South Cay, Port Royal, Jamaica, looking toward the breaker zone. The dominant coral in this region is *Diploria strigosa* which forms the large hemispheroidal brain coral colonies in the foreground. Each of these is about one meter in diameter. In the middle background is a colony of *Acropora palmata*. The depth is about two meters.

of the massive framework corals. Once it becomes established however, *Acropora palmata* quickly builds up the crest of the reef by virtue of its known fast growth (Vaughan 1915b) and the great fragility of its skeleton. This leads to the formation of extensive shallow flats such as are seen in the Ocho Rios reef where the dead coral is overgrown by *Zoanthus sociatus*. It also contributes extensively to the formation of large shingle ramparts and islands through the piling up of wave transported *palmata* rubble.

The formation of buttresses raises some important questions about the past history of Jamaican reefs. The main problem is whether the buttresses are constructional or erosional in origin.

Tracey *et al.* (1948) have described spur and groove systems formed by the profuse growth of hermatypic calcareous algae in the windward reefs of Bikini and other atolls in the Marshall Islands. These authors stated that the floor of the grooves represents an older surface upon which the algal spurs have grown. Newell *et al.* (1951) described complicated submarine trenches in shallow water on the northeastern coast of Andros Island, Bahamas. Coral and calcareous algae are sparse here and have no influence on the shape of the grooves which are believed by these authors to be caused by erosion of the underlying limestone (oölite) surface by undertows generated during storms.

In Jamaican reefs the buttress zone is formed by the vigorous proliferation of massive corals. Buttresses may develop in those regions of the reef where rapid coral growth can occur both upward toward the light and outward into the prevailing seas. Nearly all stages of the differentiation of buttresses can be observed in certain parts of the fore reef at Ochos Rios and elsewhere on the Jamaican north coast. The first step seems to be the formation on the fore reef of coral hillocks which are principally composed of one or more large heads of *Montastrea annularis*. Concomitant with an increase in height is the elongation of the coral heads by forward growth to form spurs which are oriented in a direction normal to the reef front, i.e., into the prevailing seas. Due to lateral growth, the sandy spaces between the spurs become gradually narrower until true canyons are formed with their characteristic vertical or overhanging walls. Further encroachment results in roofing over and eventual obliteration of the can-

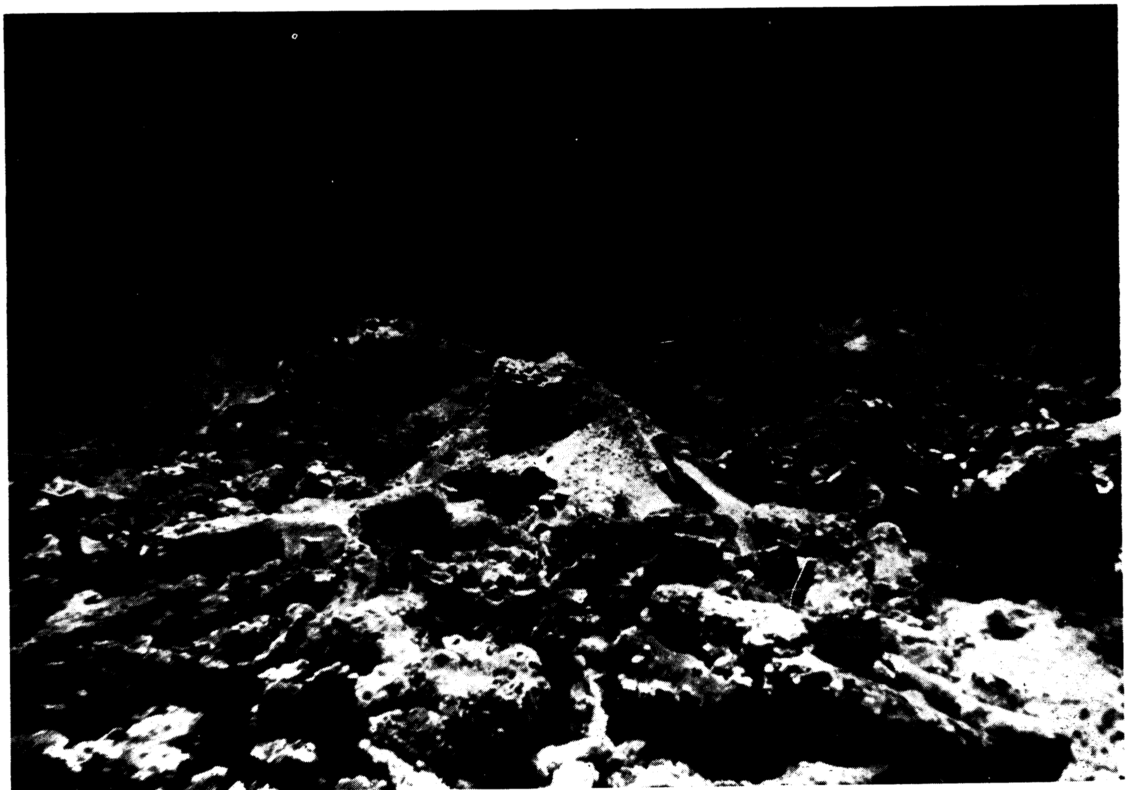

FIG. 19. Destruction of the breaker zone in the barrier reef near South-East Cay, Port Royal, possibly by the hurricane of 17 August 1951. Large overturned colonies of *Ocropora palmata,* such as those seen in this figure, occur everywhere, and in some there is an attempt at regeneration. The depth is about 2 meters.

yons. In certain parts of the reef west of Ocho Rios, many of the canyons were observed to be partially filled with detritus composed mainly of dead fragments of *Acropora palmata* which was derived from the numerous colonies of this coral that were seen growing on the tops of the buttresses in this region. By virtue of their location at the juncture of the reef crest with the fore reef, the canyons are ideal chutes which facilitate the drainage of sediment from the turbulent zones at the upper reef into deeper water by undertows set up in the breaker zone. There is no evidence that this process results in undercutting or deepening of the trenches through erosion since all the available surface area of the canyon walls is covered by living coral and is thus protected against scour.

A structure superficially reminiscent of the "room and pillar" formation described by Tracey *et al.* (1948) on the Bikini reefs was observed in Jamaica by the writer from a helicopter on the eastern side of Oracabessa harbor where the reef is protected from the prevailing seas by a promontory. Here the outer reef, corresponding to the buttress zone, is composed of huge coral bosses ranging in size from about 2 to 10 meters across and having the appearance of irregular polygons separated from each other by narrow deep rifts. Much less well defined but basically similar patterns were also seen from the air in the great reef buttress near Boscobel, Jamaica. Unfortunately, these interesting features have not as yet been explored underwater and we are unable to give any information about the nature of the coral growth in these localities.

The possibility has been considered that the buttresses may be due to secondary growth of coral on submerged cliffs previously dissected by subaerial erosion during a period of emergence. This is held to be unlikely for two reasons: first, buttresses are seen in all stages of growth and differentiation on the fore reef at the present time; and second, the geological record shows that the north coast of Jamaica has been uplifted, rather than submerged, in Pleistocene times. It is therefore likely that the buttresses are to be regarded as a growth form of a reef in a youthful and vigorous stage of its development. Nevertheless, the final answer to this intriguing question is still in the offing and waits the outcome of further investigations now planned or in progress.

Summary and Conclusions

1. Jamaica has 41 known species of shallow water Scleractinia belonging to 25 genera and 13

FIG. 20. Underwater view of the breaker zone in the Port Royal barrier reef near South Cay. The relative scarcity of *Acropora palmata* in this region is evident, the commonest coral being *Diploria strigosa* a brain coral, large hemispherical colonies of which are seen in the middle of the photo. A large head of *Millepora alcicornis* appears in the distant background. Much dead coral is seen on the bottom in the right foreground where the depth is about 3 meters.

families. Of these all except 5 species are classified as hermatypic corals.

2. The larger reefs of Jamaica are of the fringing barrier type with scleractinians as the most important hermatypic organisms. Profile traverses carried out on mature reefs demonstrate the existence of three main regions: the back reef, reef crest, and seaward slope. These in turn are divided into 7 to 9 different zones named according to their most important faunal or structural features. Going shoreward from deep water these zones are: (1) the *annularis* zone, (2) the *cervicornis* zone, (3) the buttress zone, (4) the lower *palmata* zone, (5) the upper *palmata* or breaker zone, (6) the reef flat, (7) the rear zone, (8) the channel or lagoon zone, (9) the inshore zone.

3. Observations on two representative reefs, one on the north coast and one on the south coast of Jamaica, show that zone structure and species succession is fundamentally similar in the two cases. In view of the great destruction and other changes observed on several reefs in the south coast of Jamaica it is considered likely that storms can play an important part in altering the basic pattern of species dominance and zonal succession in the upper parts of a climax reef.

4. Evidence is presented to show that *Montastrea annularis* forms the broad basis of the reef and that it is the single most important framework coral in Jamaican reefs. Colonies of this massive species grow to very large size in the seaward slope, notably in the buttress zone. In shallower water, *Acropora palmata* becomes the dominant coral. This species is important because of its abundance and the relative ease with which its colonies are broken up by heavy seas, thus readily providing the great quantities of detrital material with which the reef flat and ramparts are built up.

5. The spurs of the buttress zone are probably formed through the coalescence of large heads of *Montastrea annularis* and other massive corals. The sandy crevices between the buttresses are gradually narrowed by lateral growth of coral to form canyons. As such, the canyons probably facilitate the movement of sediments from the turbulent upper zones into the deeper regions of the fore reef. The canyons tend to be obliterated

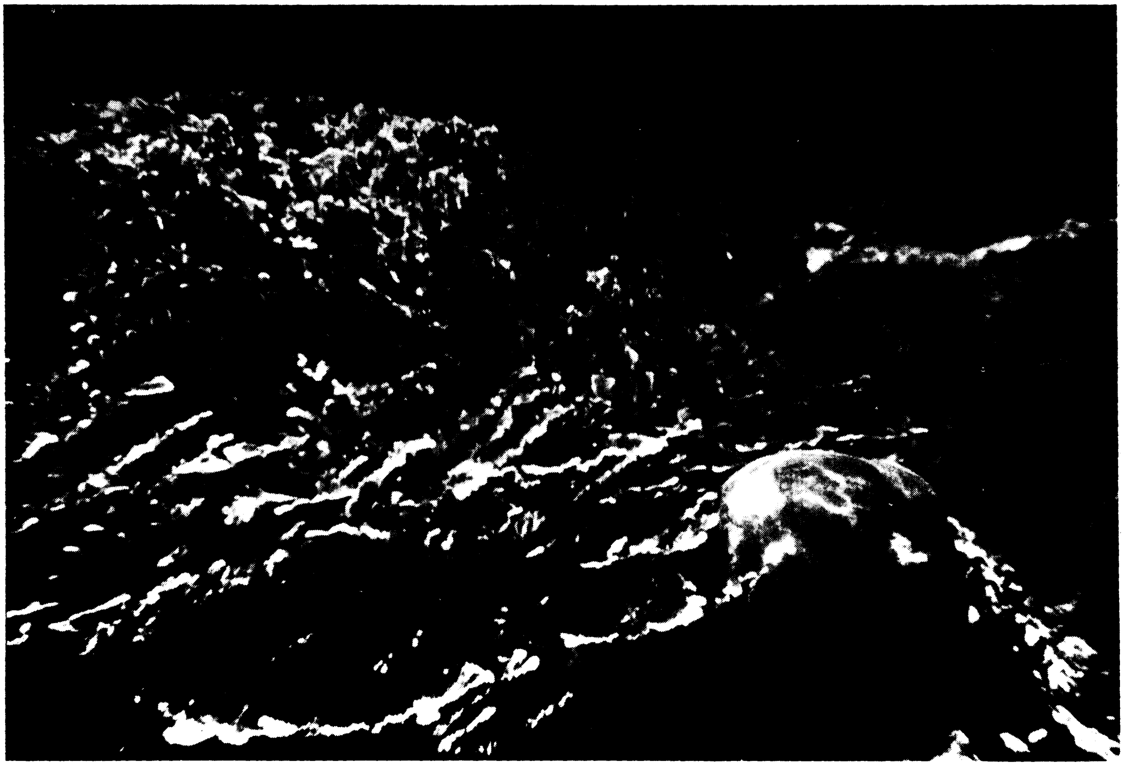

FIG. 21. Underwater view of the breaker zone of the Port Royal barrier reef near South Cay where the dominant hermatype is the hydrocoralline *Millepora alcicornis*. Very large colonies of this appear in the right background. *Acropora palmata* and a large massive *Diploria strigosa* are seen in the foreground. The depth is about 3 meters.

by a combination of overgrowth and filling in by coral broken away from the crests of the buttresses.

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AN ANALYSIS OF LEARNING IN YOUNG ANATIDAE[1]

Peter H. Klopfer
Zoology Department, Yale University[2]

Imprinting and Determination of Species-Specific Behavior

Whatever the processes involved, the young of any species must in some way come to respond appropriately to the behavior patterns characteristic of their own species if they are to reproduce successfully, while, at the same time, selective pressures maintain inter-specific differences in these patterns. In the case of extremely precocial forms like the megapodes, where incubation is by means of solar or organic heat (Frith 1956), species-specific behavior cannot be learned by the young through a physically enforced association with their parents. Conversely, a young thrush, confined by its physical condition to a nest and fully dependent upon parental care, is in a position to make ample use of conventional associative processes.

There are numerous intermediate situations. In most ducks and geese, while there may be a considerable degree of parental care, the young are nonetheless physically able to disperse several hours after hatching. Whatever bond exists to hold the young to their parents must either be present at hatching or developed within this short period. Spalding (1954), in a paper that escaped general notice until recently, described the behavior of newly hatched chickens, which tended to follow whatever moving object they first saw upon hatching. Heinroth (1910), and later Lorenz (1935), worked out details of this following-reaction, showing that the object followed formed the basis of the young's subsequent choice of a parent-*Kumpan,* and, in some instances, sex-partner. This process, which has been subjected to more quantitative studies (Jaynes 1956, Ramsay and Hess 1954, Hinde *et al.* 1956), was termed imprinting (*Prägung*), and was defined by Thorpe (1951) as follows:

> "A rapid and stable form of learning taking place early in the life of social species, whereby, often apparently without immediate reinforcement, broad supra-individual characteristics of the species come to be recognized and used as releasers."

Some workers feel that this process is not to be differentiated from a form of simple conditioning (Hinde *et al.* 1956, Fabricius 1951a), a view with which Thorpe (1956 pp. 115-118) now concurs. This view is supported by evidence that imprinting is not always as stable or irreversible as Lorenz's early papers indicated (*cf.* Stevens 1955 for an example), but certain differences from other learning processes do remain. First, imprinting is restricted to specific "critical" periods of the organism's life (*cf.* Scott and Marston 1950). Second, the reenforcement, such as it is, lies in a reafference effect, *i.e.,* the more the animal must exert itself in following a model, the more firm the bond to that model (Hess 1955). However, a final statement must await the time

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2. Present address: Zoology Department, Duke University, Durham, N. C.